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BIOLOGICAL BULLETIN

THE MORPHOLOGY OF THE MADREPORARIA. V. SEPTAL SEQUENCE.¹

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The skeleton of an ordinary polycyclic hexameral coral presents a series of septal partitions arranged in a radiating manner, and in any cycle the constituent septa are equal in size and alternate in a regular manner with the members of the other cycles. In general, the cyclic plan of a corallite is 6, 6, 12, 24, 48, etc., and the number of septa in any cycle beyond the first corresponds with the total number in all the cycles within. As the septa in any cycle are alike in size it seems reasonable to suppose that they all appeared simultaneously in the growth of a coral, a cycle at a time, and also that the inner larger cycles were developed before the outer smaller cycles; in other words, the relative sizes and positions of the septa in the mature corallite would seem to represent their order of development.

Much attention has already been given to the subject of the order of appearance of the septa in corals by different writers. The rule which Milne-Edwards and Haime give in their "*Histoire Naturelle des Coralliaires*" (1857) is well known, appearing in all text-books describing recent or fossil corals. The authors assume that in the case of the first three cycles the constituent septa of each cycle appear simultaneously, a cycle at a time, and that the relative development of each cycle corresponds with its relative size or distance from the center of the calice. From the fourth cycle outwards, however, a different sequence is

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assumed for the various members of a cycle, according to their relation to the members of the inner cycles.

Professor A. Schneider in 1871 and Professor C. Semper in 1872 also discussed the same subject. The former agrees with Milne-Edwards and Haime as regards the manner of development of the first three cycles: first a cycle of six appears, then a smaller cycle of other six alternating with the first, and later a cycle of twelve septa which are smaller and alternate with the twelve making up the first and second cycles. In the further growth Schneider considers that the septa of a newer cycle may so enlarge in size as to appear to belong to an older cycle, and thus the primary sequence and hexamerism become lost.

Semper holds that no constant rule for septal development can be established, that the manner of growth varies more or less with each species.

Professor G. von Koch, in the course of his prolonged studies on the morphology of corals, has also made certain observations upon the laws of septal development, particularly in his paper "Das Vermehrungsgesetz der Septen," 1881. His results are based mainly upon serial sections of individual coralla of *Caryophyllia*, and lead him to conclude (p. 93) in the main in favor of the validity of the sequence given by Milne-Edwards and by Schneider: "Bei den sechszahligen Korallen, sowohl den Eporosen als den Perforaten, wächst die Zahl der Sternleisten (Septa) in der Art, dass sich nahezu gleichzeitig im ganzen Umfang des Kelches zwischen je zwei älteren eine jüngere anlegt, also die Zahl der Sternleisten eines folgenden Cyclus immer gleich ist der Summe aller vorher vorhandenen. Alle Ausnahmen von dieser Regel sind auf directe Anpassungen oder erblich gewordene Veränderungen im Wachsthum des ganzen Thieres zurückzuführen."

All the above conclusions are based mainly upon the examination of adult coralla, in which there is available for comparison only the relative sizes of the septa and their order of appearance in serial sections. The actual details of growth of the septa in developing corals, in their relationships to the mesenteries, have in no instance been followed beyond the first two cycles. Professor H. de Lacaze-Duthiers (1873, '94, '97) and Professor G. von Koch (1882, '97) have both studied the early development of the skeleton in

corals, but their results throw no certain light upon the difficult problem of the manner of increase of the septa beyond the two primary cycles, nor of the relation of these to the later cycles.

Observations which I have been able to make upon the growth of the septa in larval polyps of the common West Indian coral, *Siderastrea radians* (Pallas), show the unreliability of assuming the developmental sequence from adult relationship, and give an interpretation to the later septal sequence altogether different from any hitherto proposed.

Larvæ of *Siderastrea*, fixed to fragments of glass, and capable of being examined as transparent microscopic objects, were followed in the course of their development as young polyps for a period of four months, and the order of appearance of their septa determined as far as the completion of the first three cycles.

In every case it was found that the six members composing the first cycle appeared simultaneously. This takes place shortly after the larva settles, at a stage when the young polyp has six pairs of mesenteries, arranged as in Fig. 1, where all the mesenteries are complete except the fifth and sixth developmental pairs. The septa are alike in size and situated at equal distances apart within the entocœles of the six primary pairs of mesenteries. Later development proves, as would be expected, that the six primary septa of the mature corallite are the direct enlarged representatives of the six septa first to appear in the larval polyp.

As regards the primary cycle in *Siderastrea* the surmise that adult size corresponds with developmental sequence is therefore correct. Moreover, in the early

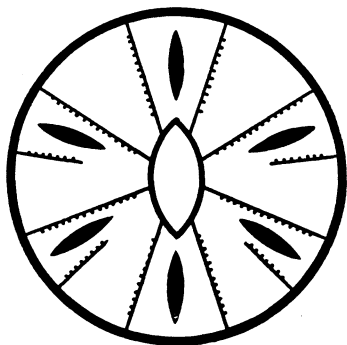


FIG. 1. Diagrammatic arrangement of the mesenteries and septa on the appearance of the first cycle of six septa. The septa are situated within the six primary entocœles, and the six alternating mesenterial chambers, devoid of septa, are the primary exocœles. The directives are situated at the opposite extremities; the two bilateral pairs of incomplete mesenteries are the fifth and sixth pairs in the mesenterial sequence. The upper border is regarded as dorsal and the lower as ventral.

stages of septal growth secured by Lacaze-Duthiers in *Astroides*, *Flabellum*, *Balanophyllia*, *Caryophyllia*, etc., and also by von Koch in *Astroides* and *Caryophyllia*, the six primary septa appeared simultaneously, and were equal from the beginning.

In *Siderastrea* the second cycle of six septa began to appear a

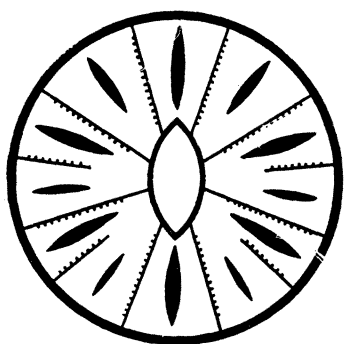


FIG. 2. Arrangement of the mesenteries and septa after the establishment of the first and second septal cycles — six entosepta and six exosepta. The dorsal pair of exosepta are somewhat larger than the middle pair, and the middle pair are larger than the ventral pair, thus giving a bilateral character to the corallum.

few days after the primary cycle, its members situated within the exocœlic chambers, thus alternating with the six entosepta (Fig. 2). In a few polyps the septa appeared simultaneously and were all practically equal, but in most individuals a marked difference was manifest; the dorsal and middle pairs of exosepta arose bilaterally in advance of the two ventral pairs, and for a time the dorsal pairs were a little larger than the middle. Within a short time the two ventral exosepta appeared, but remained smaller than the others. Thus at this early stage a decided dorso-ventrality in the development of the

septa was apparent, which gave a bilateral character to the polyp as a whole (Fig. 2).

In most of the developing corals investigated by Lacaze-Duthiers and von Koch the entocœlic and exocœlic cycles either appeared together, or one shortly after the other, as in *Siderastrea*. In most cases it was found that the members of either cycle arose simultaneously, in a truly radiate manner, without passing through a bilateral stage, though Lacaze-Duthiers figures a very decided bilateral condition in the early development of the skeleton in *Astroides* (1873, Pl. XIII., Fig. 29).

The next stage in the growth of the septa in *Siderastrea* is well defined, but is not so clear as to its significance. After the condition shown in Fig. 2 was reached the septa began to enlarge at their peripheral extremity; in some instances the enlargement

took place by the direct extension of the septa already developed, and in others by the deposition of separate skeletal nodules. The new growth was arranged in a V-shaped manner, the angle of the V being larger in the exosepta than in the entosepta (Fig. 3). In the diagrammatic figure the additions are all represented as separate calcareous fragments, but no constancy was apparent in the different septa as to the freedom or fusion of the extensions at this stage. In all the polyps the enlargement of the ventral exosepta was much behind that of the dorsal and middle exosepta, and usually it could be seen that the middle exosepta did not enlarge as rapidly as the dorsal.

At a somewhat later stage, each septum became a continuous structure, owing to the complete fusion of the free nodules in the

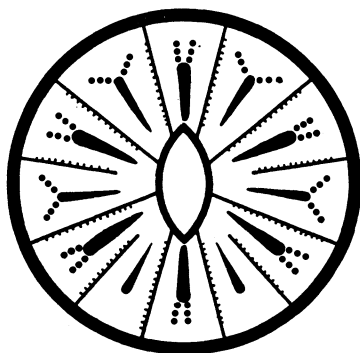


FIG. 3. Stage showing the peripheral enlargement of the septa which occurs in a bifurcating manner by the addition of separate nodules. The ventral exosepta grow more slowly than the middle and dorsal pairs.

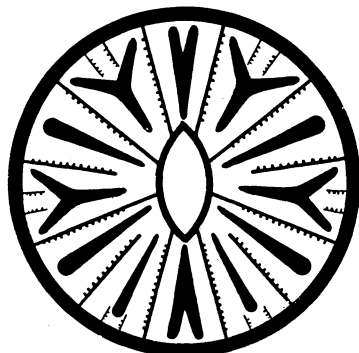


FIG. 4. Further enlargement of the septa by fusion of the nodules, and establishment of the six pairs of second cycle mesenteries; the latter, like the exosepta, decrease in size from the dorsal to the ventral border.

process of growth. The entosepta then appeared as simple formations, much broader peripherally than centrally, though the two directive entosepta showed traces of the earlier bifurcation longer than the four lateral entosepta; the exosepta, on the other hand, remained strongly bifurcated, with the exception of the ventral pair, the members of which enlarged comparatively little (Fig. 4).

A similar bifurcated stage, due to the appearance of independent calcareous nodules, occurs in the development of *Astroides*,

Caryophyllia, and some other corals, but hitherto its significance has not been satisfactorily explained. At one time the separate fragments were supposed to be concerned in the formation of the thecal wall, but it will be seen that such is certainly not their fate in *Siderastrea*.

About this time, the polyps being two months old, the second cycle mesenteries began to appear on the column wall, situated in the exocœlic chambers between the primary mesenteries (Fig. 4). In their development they also presented a conspicuous dorso-ventrality: the two first pairs appeared within the dorsal exocœles, the moieties of each pair arising at the same time and remaining equal; the two next pairs were within the middle exocœles; and finally appeared the pairs within the ventral exocœles. The dorso-ventral succession thus followed by the six pairs remained evident throughout the period under observation, the dorsal pairs being larger than the middle, and the middle larger than the ventral. The comparative development of the first and second cycle mesenteries at this period, and their relationship to the septa, are shown in Fig. 4. A similar bilateral, dorso-ventral succession of the second cycle mesenteries has long been known to occur in the development of actinian polyps, in contrast to the simultaneous origin at one time assumed.

Clearly the next skeletal stage will be one involving the establishment of septa within the entocœles of the second cycle of mesenteries, and these will constitute the second cycle of septa of the adult corallite. Hitherto it has been generally assumed that where a cycle of exosepta is already developed, and then a new cycle of mesenteries appears within the corresponding exocœles, that the exosepta already present become included within the entocœles of the new mesenteries, and thus become entosepta; an additional outer cycle of exosepta appears later and its members in their turn become entosepta. Thus Delage and Hérourard in their "Traité de Zoologie Concrète" (1901, p. 558) remark: "Quand, dans les interloges occupées par les septes du dernier cycle, naît un nouveau cycle de couples de cloisons, celles-ci se forment de part et d'autre du septa interlocaire qui, de ce fait, devient loculaire, et bientôt un nouveau cycle de septes se forme dans les nouvelles interloges qui vien-

nent d'être formées. Les cycles naissent successivement et jamais un cycle ne commence à se former avant que le précédent soit complet." Similarly J. Stanley Gardiner (1902, p. 133) in his account of the anatomy of *Flabellum rubrum* says (*italics added*): "As the growth of any corallite proceeds, more and more septa up to six cycles appear. *The former exocælic order of septa becomes entocælic by the development of new pairs of mesenteries. The increase of mesenteries takes place pari passu with the formation of new septa.*"

Unfortunately, the relationships involved in the above assertions have not been actually followed, though from the known conditions no other arrangement at first sight seems possible; and it was principally with a view to determine the truth or otherwise of the assumption that the present investigation was undertaken.

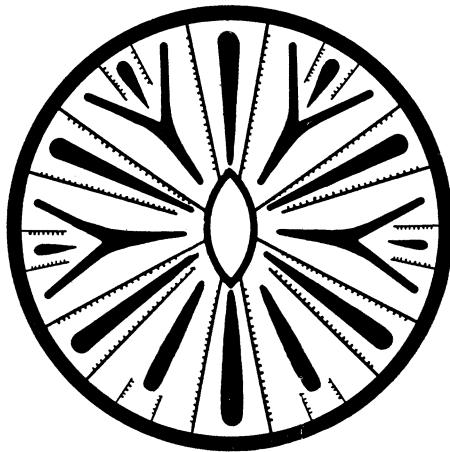


FIG. 5. First appearance of the permanent second cycle of entosepta situated within the entocœles of the second cycle of mesenteries and the bifurcations of the dorsal and middle exosepta.

Shortly after the stage represented in Fig. 4 was reached independent calcareous growths began to arise peripherally, in positions corresponding with the entocœles of the second cycle mesenteries; those within the dorsal entocœles were larger than the ones within the middle entocœles, while for a long period there was no corresponding formation within the ventral entocœle (Fig. 5). At first the structures were quite free and resembled

small independent septa ; they suggest a new series of entocœlic septa, appearing in a dorso-ventral sequence like the mesenteries with which they are associated.

Later these new septa extended more centrally, and necessarily came into union with the simple inner portions of the septa which originally constituted the exocœlic second cycle. Several of the polyps were reared until the new second and third orders of septa were fully established, when they presented the arrangement shown in Fig. 6. The peripheral, primarily independent septa

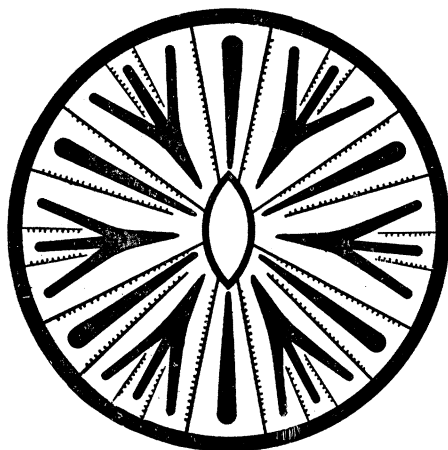


FIG. 6. Completion of the first three cycles of septa.

within the second cycle entocœles have all become continuous with the median part of the original second cycle exosepta, and along with them now constitute the permanent second cycle of entosepta ; while the bifurcations of the exosepta now constitute the third cycle of twelve septa and are seen to be exosepta.¹ It will also be seen that the growth within the ventral system has now attained the same stage as that within the middle and dorsal systems, so that the corallite as a whole presents nearly perfect radial symmetry.

The stages thus passed through are of great importance in their bearing upon several obscure points in coral development and morphology, and call for fuller consideration. In the first

¹ In the adult corallite of *Siderastrea radians* the exosepta are fused by their inner ends with the entosepta as represented in Fig. 6 and Fig. 7g.

place, it is seen that the second cycle entosepta, which are to become the permanent second cycle of the adult corallite, arise as independent formations, though later they fuse with the septa which constituted the original second cycle, the two series being situated along the same radii. They are to be regarded as altogether new formations which replace the original second cycle exosepta; the fact that they fuse with the latter in their forward growth would seem to be of incidental importance, depending upon the fact that they are in the same radii. Secondly, the original second cycle exosepta of Fig. 2 lose their morphological individuality, becoming involved in the new second cycle entosepta as the latter continue their growth centrally; they are merely the temporary predecessors of a later permanent cycle.¹ As primary second cycle exosepta they do not become included within the entocœles of the second cycle mesenteries, but only as the central continuations of the new second cycle entosepta.

The results thus afford definite proof that the exosepta of a former stage do not become the entosepta of a later stage when another series of mesenteries has appeared with the entocœles of which they correspond. It is manifest that such a conclusion could only be established in *Siderastrea* by actual observation of all the intermediate stages. When the condition represented in Fig. 6 has been reached there is no means of determining the actual two-fold origin of the second cycle entosepta. It is such conditions which have hitherto been studied, and from these no other explanation than that given by Delage and Hérourard and by Gardiner on page 70 would have been expected. Entosepta throughout would now appear to be new formations, not the continuations of the exosepta of a previous stage, and further, they arise after the mesenteries within the entocœles of which they are situated.

¹ In many corals the original second cycle exosepta appear to continue their independent growth *in situ* without losing their identity in the central extension of the entosepta. I believe it will be found that this is the true nature of *pali*, which are found in some corals as small septum-like plates in front of the larger septa. The fact that *pali* seem not to occur before the primary cycle of six septa, but only before those of later origin, is what we should expect if this surmise be correct. The primary entosepta have never had exocœlic predecessors, as is the case with the later entosepta. *Pali* would thus represent the persistent exocœlic predecessors of the entosepta beyond the primary cycle which have not lost their individuality in the later growth of the entosepta.

The significance of the twelve exosepta which constitute the outermost third cycle remains to be considered. They undoubtedly represent the direct continuations of the bifurcations of the six primary second cycle exosepta, but their relationships have now changed; instead of appearing as extensions of an older cycle of septa they themselves constitute a cycle. The details exhibited by the particular species studied seem inconclusive towards determining whether the exosepta of the later stage are to be regarded as but continuations of the exosepta of the previous stage or as entirely new formations. The former would certainly seem to be suggested; probably the point could be definitely established in some other coral species in which the exosepta in the adult are not fused at their inner extremity with the entosepta. Whichever view is accepted the exosepta of the third cycle are obviously developed in advance of the entosepta of the second cycle.¹ Thus the relative sizes and positions which the cycles will ultimately assume in the mature calice do not represent their actual order of appearance.

A third important morphological relationship is definitely established, namely, that the later septa do not arise a cycle at a time as is usually assumed, any more than do the mesenteries. Beyond the primary cycle of six entosepta, the members of which always appear simultaneously, there is a decided dorso-ventrality in the sequence of the septa of each cycle, which for the time being gives a marked bilateral symmetry to the corallum. It is only later, when the development of the septa within each sextant has reached the same stage, that an approximate equality and radial symmetry is attained. Thus the primary symmetry in corals is bilateral, and the arrangement is retained for a long period in the ontogeny of both mesenteries and septa. Therefore in the individual septa making up a cycle, as has been proved for the cycle itself, the adult size does not represent the actual order of appearance.

To return to the further development of the septa in *Sideras-*

¹ It is worthy of note in this connection that the exotentacles in *Siderastrea radians* have been found to appear throughout in advance of the entotentacles, being the only zoantharian in which this relationship is known to occur. Hence there is nothing contrary to the laws of hexactinian development in the above conception that the exosepta beyond the first series appear in advance of the corresponding entosepta.

trea. The larval polyps were not reared beyond the completion of the first two cycles of mesenteries and the first three cycles of septa (two cycles of entosepta and one of exosepta). On any colony, however, are many developing polyps which present intermediate stages between the commencement and completion of the third cycle of mesenteries and the fourth cycle of septa; and from these results have been obtained supplementary to those already presented. Mature polyps of *S. radians* have rarely more than three cycles of mesenteries and four cycles of septa (three inner cycles of entosepta and an outermost cycle of exosepta).

First, it may be ascertained what are the relationships between the third cycle exosepta of Fig. 6 and the third cycle entosepta and fourth cycle exosepta found in the mature corallite. By means of serial sections through decalcified immature bud polyps it has been possible to establish the relationship of these with respect to one another and to the new mesenteries of the third cycle. The results are diagrammatically represented in Fig. 7 (*a* — *g*), the complications due to the presence of synaptacula being omitted. Fig. *a* represents a section through an exoseptum of the third cycle, corresponding to one of the exosepta in Fig. 6, only that the peripheral extremity is now bifurcated. It is in the same stage as each of the four exosepta of the second cycle in Fig. 4, but is shown united with the calicinal wall, and no mesenteries have as yet appeared within the two limbs. Fig. *b* shows the same septum taken from a section at a higher level. Within the exocoelic bifurcation there has now appeared a pair of third cycle mesenteries, in every way comparable in their relationships to the third cycle exosepta with those of the second cycle mesenteries to the second cycle exosepta of Fig. 4.

Fig. *c*, from a still higher level of the polyp, reveals a further stage. Within the entocœle of the mesenteries is seen the rudiment of a third cycle septum. The latter is a new formation, comparable with the rudiments of the second cycle entosepta shown in Fig. 5. One limb of the exoseptum has also become free.

Fig. *d*, taken from a section above that of Fig. *c*, shows the new entoseptum becoming larger, and extending centrally further

than the mesenteries, which in their turn have also increased in size. Both limbs of the bifurcated septum are now free from the middle portion; they represent two independent exosepta becoming distinct from the single exoseptum of a previous cycle (*cf.* Fig. 6) of which they were originally continuations.

Fig. *e* is from a section through the column wall, the septa at this level being exsert, that is, extending above the calicinal wall.

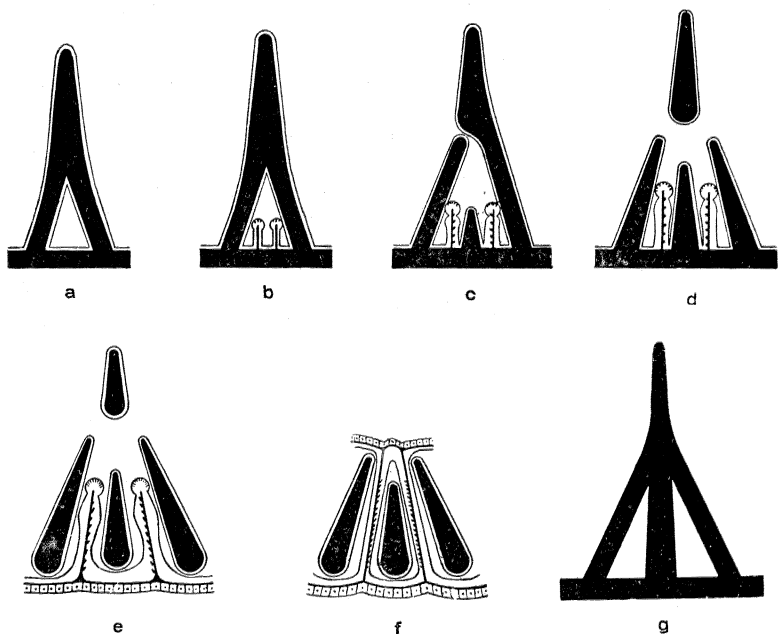


FIG. 7 (*a-g*). Series of diagrammatic figures illustrating the developmental relationships of a pair of third cycle mesenteries and a third cycle entoseptum, in association with a bifurcated third cycle exoseptum.

The relationships shown are the same as in the previous figure, but the inner radial portion of the original third cycle exoseptum has almost disappeared. Fig. *f* is through the column wall (lower) and disc (upper). The mesenteries now extend from one wall to the other, the polyp being in the retracted condition, and the entoseptum is still smaller than the exosepta, one on each side of it. It is manifest that in the later growth the entoseptum will extend more centrally, and come into union with the original third cycle exoseptum which is in the same radius (Fig. *g*), exactly as in the larval polyp shown in Figs. 5 and 6.

The series of sections thus reveals that the third and fourth cycles of septa and the third cycle of mesenteries are related in the same manner as are the second and third cycles of septa and the second cycle of mesenteries; the third cycle entosepta have third cycle exocœlic antecedents. The results may be arranged as follows:

(a) The originally simple third cycle exosepta, themselves formed as bifurcations of simple second cycle exosepta, become bifurcated at their peripheral extremity.

(b) Within each bifurcation there appears a new pair of third cycle mesenteries, and then within the entocœle of the pair is formed a third cycle entoseptum.

(c) The new entoseptum fuses with the central portion of the third cycle exoseptum, while the bifurcations of the latter constitute two new exosepta of the fourth cycle, and are fused at their inner extremity with the entoseptum embraced by them.

Presumably the same process as above outlined will be followed within the two exocœlic chambers of each sextant of the polyp, so that in the end there will be twelve entosepta forming the completed new third cycle and twenty-four exosepta forming the completed new fourth cycle.

The actual sequence according to which the third and fourth cycles of septa are formed remains to be noticed.

The septa alone in the dried corallum are insufficient for this purpose, as they afford no certain means by which the directive axis can be determined, and from this the dorsal and ventral borders of the calice. It has been shown, however, that the mesenteries associated with the entosepta appear in pairs only a little in advance of the entosepta within them; therefore if the sequence of the mesenteries be determined it can be assumed that the septa follow the same order.

From colonies of *Siderastrea* sections of a large number of bud polyps at different stages of development have been prepared, and from these it has been possible to determine the order of appearance of the twelve pairs of third cycle mesenteries. This is indicated in the series of diagrammatic figures in Fig. 8 (a-d). In Fig. 8 a, in addition to the primary and secondary cycles, a pair of third cycle mesenteries (III.) has appeared on each side of the median axis, situated in the exocœle between

the dorsal directives and the dorsal pair of second cycle mesenteries. Such an early stage is to be expected on the dorso-ven-

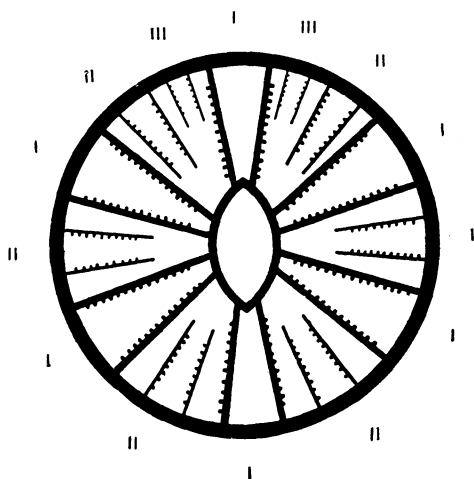


FIG. 8a.

FIG. 8 (*a-d*). Series of diagrammatic figures illustrating the order of development of the twelve pairs of third cycle mesenteries.

tral succession already established in the case of the second cycle mesenteries (p. 70).

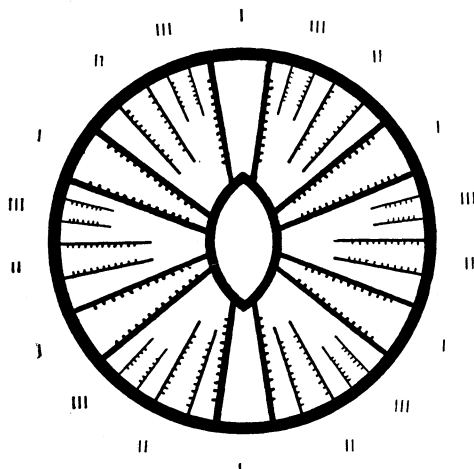


FIG. 8b.

The succeeding exocœlic chamber on each side lies between the dorsal pair of second cycle mesenteries and the dorso-lateral

pair of first cycle mesenteries, and it might be supposed that the new mesenteries would occupy the exocœles in regular succession from one aspect of the polyp to the other. Instead of this

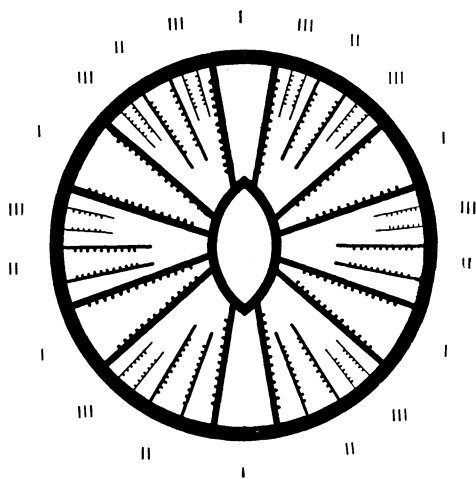


FIG. 8c.

the pairs are found to arise successively within only the dorsal member of the two exocœles of each system. This is shown

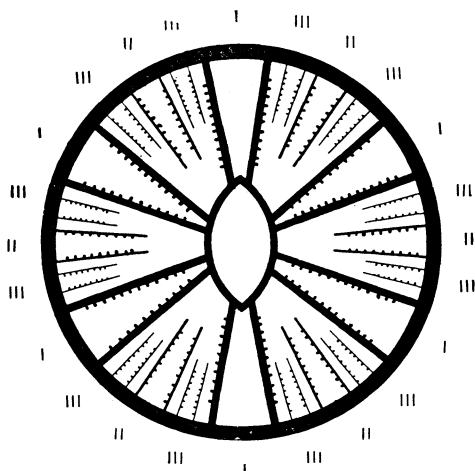


FIG. 8d.

in the next stage available, Fig. 8b, where a third cycle pair is found within the dorsal exocœle of each sextant.

A further stage secured in the growth of the twelve pairs of third cycle mesenteries is given in Fig. 8*c*, where a pair has appeared on each side within the ventral exocœle of the dorsal sextant. Clearly, if the succession thus indicated were followed with perfect regularity, other pairs would appear within the ventral exocœles of both the middle and the ventral sextants, and the cycle would then be completed according to Fig. 8*d*. No stage exactly corresponding with Fig. 8*d*, however, has been obtained, as the polyps of *S. radians* very rarely, if ever, complete the third cycle of mesenteries. Still the sequence so far as it can be traced is such as to warrant the conclusion.

The regularity in the dorso-ventral sequence of the mesenteries shown in Fig. 8 was secured only after an examination of a number of polyps. In a colony in which the polyps are so closely arranged as in *S. radians* the individuals are rarely found to undergo their later development with perfect regularity all round; some regions will be in advance of the normal sequence and others behind. The polygonal form assumed by the adults is evidence that a certain pressure is exerted upon a form which would otherwise be circular, as in the simple polyps reared from larvæ. Spatial difficulties may therefore be held sufficient to account for the irregularities appearing in the growth of the third mesenterial cycle. In *Astrangia solitaria* and *Phyllangia Americana*, where the polyps are practically free from one another, and retain their cylindrical form throughout, the regularity of development from one border to the other is more pronounced, and I have found (1902, p. 459) the order of appearance of the mesenteries to be the same as that established for *S. radians*.

The normal sequence of the third cycle mesenteries in *Siderastrea* being now established we are justified in assuming that a like succession will be maintained by the third cycle septa, as individually the septa arise shortly after the mesenteries with which they are associated. Hence the normal sequence for the members of the first three cycles of entosepta will be that represented in Fig. 9. The six septa of the first order of entosepta (I.) appear together as a cycle; the six members of the second (II.*a*–II.*c*) follow a simple dorso-ventral succession; the twelve members of the third order (III.*a*–III.*f*) also appear in a dorso-

ventral succession, but in two series — first a series of six (III.*a*–III.*c*) within the dorsal of the two interspaces in each sextant, and then the remaining six (III.*d*–III.*f*) in a like order but within the ventral of the two interspaces. As explained below, the exosepta (X.) constituting the last outermost cycle have not the same ordinal significance as the entosepta.

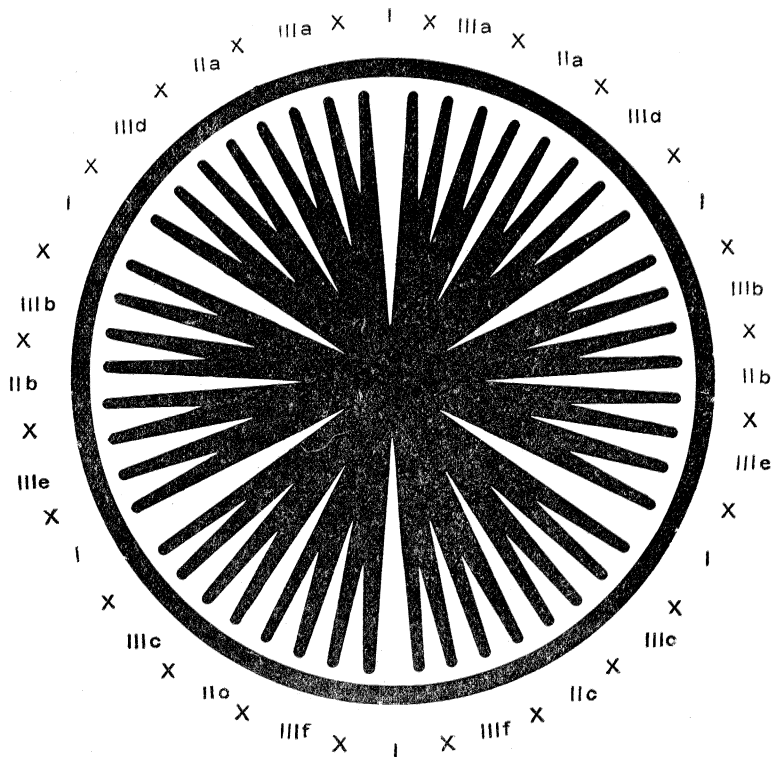


FIG. 9. Diagram showing the order of appearance of the septa in a corallite with three cycles of entosepta (I.-III.) and an outer cycle of exosepta (X.). The Roman numerals indicate the cycle to which the septa belong and the letters their sequence in the cycle.

Studies on the mesenterial sequence of other corals indicate that a similar septal succession will in all probability be followed by most forms in which the adult calice shows a regular hexamerous cyclic plan. Individual departures from the order may be expected, but are to be looked upon as irregularities; regularity of growth of the higher cycles of mesenteries and septa is

by no means so pronounced as in the first and second cycles which are less likely to be influenced by spatial considerations. The sequence given is altogether different from anything which has hitherto been surmised for any coral, and further studies are desirable to determine how far it admits of general application in the group.

From what has already been revealed it is manifest that the exosepta of corals do not possess any true ordinal sequence comparable with that of the entosepta. Exosepta have been found to be present at each developmental stage, always constituting the outermost cycle, and equalling in number the sum of the inner entosepta ; but until the adult condition is reached they are merely the predecessors of the entosepta. We may consider them as the direct continuations of the primary six exosepta which bifurcate at each stage, or, less likely, as arising anew with each cycle of entosepta. Regarded as the persistent representatives of the primary exosepta they more nearly conform to the "law of substitution" in actinian tentacles as established by Lacaze-Duthiers (1872) and Faurot (1895).¹

Studies on other corals, as well as considerations on the tentacular development in actinians, suggest that the exosepta may arise in different ways in different species of corals, and that a more

¹ In actinians generally it is found that after the protocnemic stage the tentacles appear two at a time, one entocœlic and one exocœlic, corresponding with the two chambers formed upon the appearance of a new pair of mesenteries ; sometimes the entotentacles appear in advance of the exotentacles, though in *Siderastrea radians* the reverse is the case. The entotentacles when established are larger than the exotentacles, the length of the former being in accordance with the order of appearance of the cycle to which they belong, the largest being the first to appear. The exotentacles all attain an equal length and throughout are relegated to the outermost cycle, whatever be the cycle of entotentacles with which they first appeared. They constitute a single cycle of which the members are smaller than those of the cycle of entotentacles last to appear. The number of exotentacles in the last cycle is always half the total number of tentacles, the number of exocœles being equal to that of the entocœles.

Being soft polypal structures it is easy to understand how as new entotentacles are added the exotentacles become pushed aside and thus occupy different radii at different times. The septa, being hard fixed structures, do not admit of rearrangement ; the new growth has to be adapted to the old, as in the fusion of the new entosepta with the old exosepta.

The tentacles, like the septa, thus arise in such a manner that it is impossible to determine their order of development from their relationships in the mature polyp.

precise significance as to their relationships at different stages may be forthcoming than is possible in *Siderastrea*. There are indications that in some forms an entoseptum and an exoseptum arise together, thus more closely recalling the method followed in the appearance of the tentacles.

The relationships now proved to exist between the entosepta and exosepta of corals involve important considerations when the cyclic hexameral sequence is not completed in the mature corallite, a condition which almost invariably happens in *S. radians*, as well as in numerous other corals. As regards both septa and mesenteries it is found in such cases that the last cycle is rarely a multiple of six, but some irregular number, resulting from the fact that at maturity the polyp does not complete the last cycle begun. Exosepta have been shown to appear always in association with entosepta, whatever be the number making up a corallite, and, as often remarked, the two series are equal in number and the exosepta outermost in position. Hence it follows that in the cyclic incompleteness of the mature corallites of *Siderastrea* the third entocœlic cycle and fourth exocœlic cycle of septa vary in the same degree; whatever number of entosepta be lacking to form the complete third cycle of twelve a like number will be wanting from the twenty-four exosepta which should form the fourth cycle.

When describing the number of septal cycles within a calice of which the cyclic hexameral plan is incomplete it is usual in systematic works on corals to regard the hexameral multiples as completed so far as the number of septa will permit, and then to relegate to the last cycle all the surplus septa not included in the hexameral formula. The cycles are all supposed to be hexamerously complete with the exception of the last. Thus, with regard to *S. radians*, Milne-Edwards states: "Three cycles of septa complete, and, in general, a variable number of a fourth cycle"; likewise Verrill (1901, p. 133), describing the same species, says: "They [the septa] form three complete cycles, with part of the fourth cycle developed, so that the number is usually 36 to 40."

The relationships now established between the entosepta and

exosepta indicate that the above formulæ do not express the true morphological character of the septa. Any hexameral incompleteness in the number of septa making up a corallite affects both the entosepta and the exosepta, that is, both the penultimate and the last cycles; if any septa be wanting to complete the hexameral multiple of the last cycle of entosepta the same number will be wanting from the outermost cycle made up of exosepta. The third complete cycle as understood by Milne-Edwards and by Verrill is really made up of both tertiary entosepta and of tertiary exosepta. The two kinds of septa are obviously of very different value in their development and relations to the mesenteries, and, as a matter of fact, will scarcely be of the same thickness and radial length to justify their being regarded as members of one cycle.

The cyclic formula, as usually understood in systematic works, may be written, 6, 6, 12, X , where X will represent any number from one to twenty-four. Formulated in this way the number 12 conveys the impression that the third cycle is really completed, that all the remaining septa belong to the next or fourth cycle, and that it alone is numerically incomplete. But beyond the two first cycles the septa of the penultimate and last cycles are formed concurrently, or almost so, in pairs, and incomplete cyclic hexamerism, as met with in *S. radians*, is really an intermediate condition in the establishment of two adult hexameral cycles, not of one alone, and attention should be drawn to this in the septal formula.

According to the relationships above established the morphological septal formula for *S. radians* should be written 6, 6, X , $6 + 6 + X$. In this formula the numbers 6, 6, represent the septa in the first and second completed entocycles, and X the number in the third entoseptal or penultimate cycle which does not yet complete the hexameral sequence; while $6 + 6 + X$ will represent the total number of exosepta, X being the same number as before. In the calice some of the exosepta will be tertiaries and some will be quaternaries, the number of the latter being always double the number of tertiary entosepta. The formula for a corallite having 36 septa would, according to the ordinary cyclic formula, be written, 6, 6, 12, 12, whereas, con-

sidered as entosepta and exosepta, the formula would be 6, 6, 6, 18; the three first numerals in the latter indicate the entosepta and the last the exosepta. The cyclic formula of a corallite with 40 septa would be 6, 6, 12, 16, and the morphological formula 6, 6, 8, 20. In the first morphological formula 12 of the exosepta will be quaternaries and 6 will be tertiaries; in the second 16 will be quaternaries and 4 tertiaries.

Where the relationships of the septa to the mesenteries are clearly known the morphological formula will more nearly express the real value of the septa than the ordinary cyclic formula, the latter has little significance unless the hexameral sequence is fully completed. One is not justified in saying that a cycle is really complete unless all its constituents have the same morphological value, and this is not the case when some are entosepta and some are exosepta.

A few remarks may here be made concerning the dorso-ventral appearance of the organs in corals generally, and the consequent marked bilaterally of the calice for the time being.

In palæontological literature much has been made of the fact that the Palæozoic rugose corals (*Tetracoralla*) are bilaterally symmetrical, while most modern corals are radially symmetrical. The results here outlined prove however that modern corals are strongly bilateral in the course of their development, and that it is only when the septa are fully established that an approximate radially is assumed. In like manner I have found that many rugose corals attain perfect or almost perfect radially when maturity is reached, though the developmental stages are strongly bilateral. Radially in the *Actinozoa*, as compared with bilaterality, seems to have a more ontogenetic than phylogenetic significance. Furthermore, beyond the six primary members the septa in the *Rugosa* are added in a manner altogether different from that in modern hexameral corals, hence the bilaterality of the one group has a different origin from that of the other. The subject of bilaterality in the *Rugosa* will be more fully discussed in a later paper.

In modern corals the bilaterality of the polyp during development may be looked upon as associated in turn with each cycle

individually. Any cycle of septa or mesenteries tends to attain its radial condition before the next cycle commences to form, when the additions take place in such a manner as to again confer bilaterality upon the polyp as a whole. Thus the first two cycles of septa become truly radial before an additional cycle commences, when the growth of this is continued in a bilateral manner; likewise the new second and third cycles assume their radial stage before the members of the fourth cycle made their appearance, these also proceeding from one border to the other. In like manner the first cycle mesenteries are nearly radial before those of the second cycle arise and introduce a conspicuous bilateral symmetry; on the second cycle mesenteries assuming the radial plan the third cycle members begin to appear, again in a bilateral manner.

The successive dorso-ventral growth followed by the constituent mesenteries and septa of each cycle also confers a certain individuality upon the cycle. The different cycles, arising independently, seem to represent so many distinct recurring phases of growth in the life of the polyp; they do not constitute a continuous addition from one border to the other, as is usual in permanently bilateral animals, particularly segmented forms. The members of a cycle appear in a dorso-ventral sequence and may retain their differences in size for a long time, but in the end they become equal and thereby confer radial symmetry upon the polyp. Then another cycle commences to form in somewhat the same bilateral dorso-ventral succession, displays for a time the consecutive origin of its members, and afterwards attains radially.

The conception of recurring phases of growth in cyclic coral polyps is best realized when comparison is made with the mesenterial increase characteristic of the *Cerianthæ* and *Zoanthæ*. In the former the mesenteries beyond the protocnemes always develop in a regular bilateral successive manner, from the dorsal (anterior, sulcar) to the ventral (posterior, asulcar) aspect, the oldest being dorsal or anterior and the youngest ventral or posterior, recalling more the method followed by segmented animals; there is in the *Cerianthæ* never a reversal of growth to the anterior end, followed by a successive series to the other, such as occurs in ordinary hexactinians. Employing the term "band of

proliferation," introduced by van Beneden in 1897, we may say there is only one median band of proliferation in cerianthids, while in hexactinians there are many such bands occurring all round the polyp, the number increasing with age — at first six, then twelve, twenty-four, etc.

In the Zoantheæ also mesenterial development is always in the same succession after the protocnemic stage. The increase takes place within only two of the six primary exocœlic chambers, one on each side of the ventral directives; there are only two bands of proliferation or zones of growth. In this case, however, the order followed by the new mesenteries differs from that in hexactinians and cerianthids; it proceeds from the ventral (posterior, sulcar) to the dorsal (anterior, asulcar) aspect of the polyp, not from the dorsal to the ventral.

The bilateral development of the organs, from one border of the polyp to the other, in ordinary actinians and corals would seem to have no phylogenetic significance beyond the group of the cœlenterates; indeed, even here we appear to have as yet no definite understanding as to what its meaning may be. The approximate radial symmetry of adult cœlenterates is assumed from very diverse developmental conditions (*cf.*, hexactinians, zoanthids, cerianthids, and the tentacles and other cyclic organs in the Hydromedusæ and Scyphomedusæ). Whatever may be said in favor of the well-known view that the mesenterial arrangement in cerianthids suggests the metamerism of higher animals there is clearly no support for such a conception in the development of the organs in hexactinians. In this latter group we are concerned with a radial cyclic repetition of the organs, even though the members of each cyclic series arise in bilateral succession from one border to the other.

SUMMARY.

1. In the coral *Siderastrea radians* the six members of the first cycle of septa appear simultaneously, shortly after fixation of the larva, situated within the entocœles of the first cycle of mesenteries.
2. Six members of a second cycle are developed within the primary exocœles shortly after the primary cycle of septa. They are the temporary predecessors of a later permanent cycle,

and arise either simultaneously or in bilateral pairs in a dorso-ventral order. Later, they become bifurcated peripherally, either by the direct extension of the original septum or by the production of separate fragments which subsequently fuse. The bifurcations also appear in a bilateral dorso-ventral order.

3. The six members of the permanent second cycle of entosepta arise within the entocœles of the second cycle mesenteries soon after these make their appearance. The two right and left dorsal septa appear first, then the two middle members, and, at a much later period, the two ventral, the series thus exhibiting a decided dorso-ventrality. In the end they become equal, and each fuses with the central part of the corresponding second cycle exoseptum previously developed, these exosepta thereby losing their individuality.

4. Twelve members of a temporary third cycle are situated within the exocœles between the primary and secondary pairs of mesenteries, and represent the bifurcated extensions of the six primary exosepta. The original second cycle exosepta thus become the third exocœlic cycle, their place having been taken by the new second cycle of entosepta.

5. A new third cycle of twelve (or less) septa arises on the appearance of the pairs of third cycle mesenteries, in a similar manner to that followed by the second permanent cycle. New entosepta appear within the entocœles of the third cycle mesenteries, and the bifurcations of the third cycle exosepta then become the exosepta of the fourth cycle.

6. The third cycle entosepta, following the mesenteries, are developed in a bilateral dorso-ventral order, but in two series; first a series within the dorsal moiety of each sextant, and then a second series within the ventral part of each sextant.

7. Exosepta are present at each cyclic stage in the growth of the corallum, alternating in position and corresponding in number with the sum of the entosepta. They never become entosepta, but always constitute the outermost cycle of shorter septa; only the entosepta have any ordinal significance. Until the adult condition is reached the exosepta are the temporary predecessors of the entosepta. The developmental relationships between the entosepta and exosepta are closely comparable with

those between the entotentacles and exotentacles. The law of substitution, first discovered by Lacaze-Duthiers for the tentacles of *Hexactinæ*, is thus found to hold also for the septa.

8. Where the cyclic hexamerism of a corallite is incomplete the ordinary cyclic formula does not express the true relationships of the septa; the entosepta and exosepta vary in the same degree, so that the true morphological septal formula for a corallite with three cycles and part of another is 6, 6, X , $6 + 6 + X$, where X may be any number from 1 to 12.

9. The cycles of septa and mesenteries represent so many distinct recurring phases of growth at intervals all round the polyp, not a continuous increase from one extremity to the other as in metameric animals. With the exception of the first the members of each cycle follow a dorso-ventral succession, display a bilateral symmetry for some time, and ultimately assume an approximate radial plan. The succession for the third cycle of entosepta is two-fold.

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